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THE BOTANICAL REVIEW

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THE RÔLE OF LIGHT IN THE LIFE OF PLANTS

I. LIGHT AND PHYSIOLOGICAL PROCESSES

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The physiological activities, characteristic growth and differentiation of plant species are brought about by the interaction of all the many factors of inheritance and environment. No one factor taken alone and divorced from all other contributory conditions, such as light, temperature, moisture, minerals, etc., can be considered as being significant in the life of plants. All variables work together and each shares to a greater or lesser extent in the different processes which determine the morphological destiny of the growing plant. Along with other components of the environment, light is known to have profound effects upon the properties of matter and it should be expected, therefore, to have an important influence upon living organisms. A great volume of literature has been written concerning the action of sunlight and artificial light upon plants, so that it is possible to review here only certain selected contributions to the general subject. In the first part of this paper, the rôle of light will be discussed in relation to some of the vital processes, physical properties and chemical constituents of plants,

while the second half of the paper, to appear in a later number, will be devoted to a consideration of the influence of light upon their gross size, form and microscopic structure.

RELATION OF LIGHT TO BIOLOGICAL PROCESSES

The source of energy for the plant world is the sun. "Sunlight" comes to the earth's surface in electromagnetic waves varying in length from about 2,900 to approximately 20,000 Ångströms. An Ångström, which is the unit of wave length in common use, is equivalent to 1×10^{-10} meter. Wave lengths of radiation are often measured and recorded also in other terms, such as thousandths (μ) or millionths ($\mu\mu$ or $m\mu$) of a millimeter. For example, a wave length (λ, Greek letter lambda) of 10,000 Ångström Units (Å. U.) = 1,000 millimicrons, $m\mu$) = 1 micron (μ). The quality, intensity and duration of solar radiation at any point on the earth's surface vary in a definite manner with the time of year, altitude and latitude, and may be modified, further, by atmospheric absorption and scattering and by local obstructions due to topographical features, plant formations, etc. (235, 289). The value of solar radiation at sea level is approximately 1.5 gram calories per square centimeter per minute which corresponds to 10,000 foot candles in terms of illumination (235). Of the total radiation reaching the earth from the sun, about 60 per cent is infra-red, approximately 1 per cent is ultra-violet and the remainder is visible light. Only

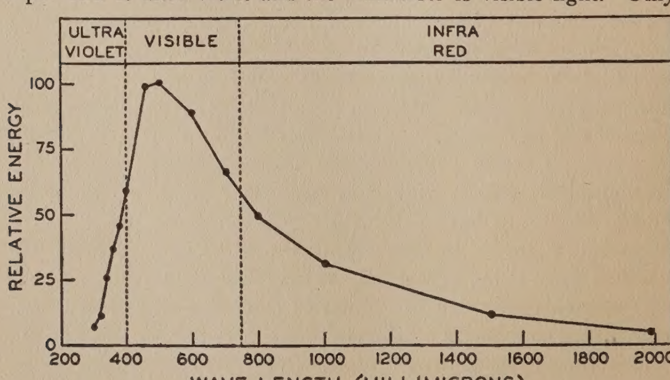

FIGURE a. Distribution of energy in the ultra-violet, visible and infra-red regions of the solar spectrum at the earth's surface. From Fowle (133).

the visible portion of all the solar radiation, *i.e.,* that fractional part (about 0.75 to 0.4 μ) which produces the sensation of light in the human eye, should be regarded strictly as sunlight. However, the word *sunlight* is commonly used to mean solar radiation in a general sense. In recent years, many different kinds of artificial light sources have been used in the growth of plants under various conditions. The wave length and energy distribution of these lamps vary widely, depending upon their temperature and the characteristic emission spectra of the elements employed in their operation (*cf.* 289). Visible radiation is of vast importance in the synthesis of carbohydrates and in its formative effects upon the development of plants. Furthermore, those radiant waves of energy which are shorter (ultra-violet) and longer (infra-red) than the visible rays may be detected and measured by convenient methods, and are known to bring about photochemical and heat effects of considerable importance to plant life.

Researches in the field of photobiology have led to the discovery that the life processes which are influenced by light take place in an orderly fashion, permitting the formulation of laws which precisely describe the biological effects as related to the radiant energy. As evidence of photic stimulation in plants one may observe the products of chemical reactions, tropistic and tactic responses, growth rates, etc. That light must be absorbed in order to produce an effect was first enunciated clearly by Grotthus in 1819 (173). Thus, blue starch iodide is decolorized by yellow light, yellow gold chloride by blue light, and red ferric thiocyanate by green light. Each is attacked by its complementary color, *i.e.,* by the light which it absorbs. The applicability of the Grotthus law has been found true for many biological phenomena, *e.g.,* photosynthesis of carbohydrates by green plants (554, 555), inactivation of enzymes by ultra-violet radiation (153), hemolysis of red blood cells by sunlight (274), etc.

Another law, which was originally proposed by Bunsen and Roscoe (60) for the darkening of silver chloride paper and which is now a well known principle in photochemistry, states that to produce a definite photic effect a constant amount of energy is necessary regardless of its distribution in time. If I is the intensity and t the time of its action, then $It = C$, where C is a constant. This law is applicable to simple direct photochemical reactions

where the velocity is proportional to the intensity. As examples of physiological processes which illustrate the Bunsen-Roscoe law, there may be mentioned the phototropic response of the *Avena* coleoptile (31) and the minimum stimulation of *Mya* by light (191). Another well known principle in animal physiology is Talbot's law which states that a reduction in the time of action of light is equivalent visually to a corresponding reduction in its intensity (*cf.* 192). Whether the intensity is adjusted by rapidly interrupted illumination (as with a rotating sector disc) or by other means, using continuous light, the photosensory value is found to be the same. Rao (421) has reported the validity of this law for the action of light upon seed germination of *Lythrum salicaria.*

Not infrequently, however, some other mathematical relationship is found to exist between the strength of the stimulus and the response. When the magnitudes of the response are plotted against the logarithm of the stimulus and a straight line is obtained, their relationship is frequently referred to (perhaps incorrectly) as the Weber-Fechner law (124, *cf.* 192). For example, the reaction time in the dark-growth response of *Phycomyces* is proportional to the logarithm of the preceding light intensity (69), and the creeping responses exhibited by many animals are known to be proportional to the logarithm of the intensity (88, 382, 575) of the stimulus. It appears that this law frequently holds true only for stimulation of a certain range and may not apply to relatively low or high intensities. In still other instances none of these simple laws can be applied to more complicated circumstances, as, for example, in the photeolic movements of *Mimosa* (64) and in the light inhibition of seed germination in *Phacelia tanacetifolia* (363), etc., where the responses appear to be hyperbolic functions of the stimuli.

According to the quantum theory of Planck (*cf.* 592), radiant energy consists of small definite units, the absolute size of which is defined by the equation $E = hv$, where E is the quantum (or energy unit), v is the frequency of the wave, and h is Planck's constant (6.5×10^{-27} erg/sec). The quanta (E) of short waves, where v is greater (since the frequency = velocity/wave length), contain more energy than the quanta of longer wave lengths. The same energy value of violet light of λ .4 μ contains only half as many quanta as an equivalent energy value of red light of λ .8 μ. Furthermore, it

has been found that the intensity of the reaction depends, not upon the size, but upon the number of absorbed quanta. One hundred quanta of λ .4 μ may accomplish the same work as 100 quanta of λ .8 μ, though the energy of the latter is only half as much. This is the well known law of photochemical equivalence (115) which states that one quantum of radiant energy must be absorbed by each molecule of the photo-reacting material. In other words, reaction rate is proportional to density of absorbed radiation. Not many biological processes have been investigated from the standpoint of quantum activation but it appears that the photochemical equivalence law applies to carbon assimilation (570, *cf.* 222), to photic activation of light sensitive seeds (249), etc. This law, which has formed the basis for a rational development of photochemistry since 1912, would upon proper investigation no doubt be found applicable to many other photosensitive systems in plants.

According to physical theory, matter consists of positive nuclei about which rotate (or oscillate) negative electrons. When the charges are grouped in stable states, which do not radiate, matter exists as atoms and molecules. Atoms are capable of passing from one stable state to another stable state with great rapidity through changes in the electronic orbits. According to Bohr's theory (*cf.* 592), when radiant quanta of a suitable frequency are absorbed by these elementary oscillators the orbits are increased and when radiation is emitted from atoms the orbits are decreased. The phenomena of radiation and absorption may be considered, then, as related to the reversible change in the diameter of the electronic orbits about their nuclei. Absorption of radiant energy by the chemical constituents of plants is dependent upon frequency of oscillation of the electrons of the system, the phase and intensity of radiation, and probably other factors. Once absorbed, the energy may be dissipated as heat to cause a temperature rise, or it may be re-radiated, as in the phenomenon of fluorescence, or chemical reactivity may be brought about by virtue of the active state of the atoms or molecules (*cf.* 185). A formal classification of the different groups of photochemical reactions, as proposed by Weigert (*cf.* 22), would include simple and complex reversible reactions which involve an increase in energy, irreversible coupled reactions with loss of energy in which the products of the photochemical change are used up in other reactions, and irreversible catalytic re-

actions with loss of energy in which the catalyst may exist only during illumination or may remain after the action of light. One of the outstanding characteristics of straight photochemical reactions is their relation to temperature. Their temperature coefficients are very near 1 for 10° C. in contrast to ordinary chemical reactions which double or treble for a rise of 10° C. (*cf.* 192). An extended discussion of the properties of radiation is not possible here. There are numerous special treatises for fundamental information concerning the theory and technique of light as applied to problems in general physiology (*cf.* 239, 265, 289, 367, 394, 395, 415, 512, 596.

PHOTOSYNTHESIS

Through the action of light in the formation of specific chemical substances, such as pigments, hormones, carbohydrates, etc., profound influences are brought to bear, not only upon processes of growth, but also upon processes concerned in the differentiation of specialized cells and organs, and the general course of development in the whole plant. The relation of solar energy to certain chemical constituents and physical conditions which influence the growth habit, cellular structure and reproductive stages in plants deserves special consideration.

One of the most important functions of light in relation to green plants is that concerned with photosynthesis of carbohydrate food which constitutes the supply of energy for growth and development. The nature of the chemical process and the conditions under which photosynthesis takes place in living green plants have been studied by numerous investigators, each attacking a certain aspect of the general problem. The structure of chlorophyll and its characteristic absorption of light energy which drives the mechanism has been elucidated by Willstätter and Stoll (588). The effectiveness of different regions of the spectrum has been worked out on a quantum basis by Warburg and Negelein (570) who reported that five quanta of blue and four of red light were necessary to reduce each molecule of CO_2. On a basis of equal energy absorption green light appears to be between the red and blue in its efficiency for photosynthesis (62, 140). Recently, Emerson and Arnold (119), experimenting with effects of intermittent red light, have been able to produce convincing evidence for the existence of two sepa-

rate phases in the process, *i.e.*, the photosensitive phase, activated by light and completed in a small fraction of a second, and the slower chemical phase which may be completed in darkness and which is known as the "Blackman reaction" after the name of its discoverer. With flashing light it has been possible to increase the photosynthesis of sugars per light unit by as much as 400 per cent. The biological aspects of photosynthesis have been dealt with in a long series of investigations by Lubimenko (283) and his associates. This work has been reviewed recently by Priestley (411). The effects of limiting factors in carbon assimilation have been studied by Blackman (33), Lundegardh (291), Van den Honert (207), Van der Paauw (375, 376), etc. Stiles (526) and Spoehr (514) have written monographs reviewing the whole subject in a comprehensive manner. Recent papers by James (222) and Baly (19) treat the dynamical aspects of photosynthesis in a critical fashion, so that extensive discussion of the process seems unnecessary here. The amount, kinds and position of the products of photosynthesis in the plant depend upon the factors concerned in their formation, the enzymes present, the structural pathways for translocation, the relative rates of oxidation (respiration) and reduction (CO_2 assimilation), etc. The importance of photosynthesis for the present discussion is that food is made available for growth through the action of light upon the chlorophyll apparatus.

CHLOROPHYLL FORMATION

The relation of radiation to pigmentation is of very great importance through the necessity of light for formation of pigments, and due to the fact that pigments absorb radiant energy which is essential for physiological activities of plants. Naturally occurring plant pigments, which are found in the protoplasmic structure of the higher plants, are chlorophyll, carotin and xanthophyll. In the sap occur the water soluble pigments, *e.g.*, anthocyanins, flavones, flavonols, etc. In lower plants, such as algae and bacteria, still other pigments are found, as the carotinoid fucoxanthin of the brown algae and the proteinaceous phycoerythrin and phycocyanin of the red and blue-green algae. The last two pigments have been studied extensively by Svedberg (529). The effect of light upon chromogenesis and the possible rôles of diverse types of pigmentation will be discussed briefly.

In the great majority of plants, light is essential for proper development of chlorophyll, though this is not true of seedlings of *Picea,* sporelings of many ferns and mosses (85, 283, 411, *cf.* 291) and some species of unicellular green algae (316). According to Eyster (123), the precursors of chlorophyll may be formed by angiosperm seedlings in darkness and in the presence of light this "protochlorophyll" is changed into green chlorophyll. Temperature affects this dark process but the photochemical change of the precursors to the green pigment is uninfluenced by temperature (284). It is generally considered that in intense light, formation and decomposition of chlorophyll go on simultaneously, and the net concentration of chlorophyll increases with light up to a certain optimum above which the chlorophyll amount is inversely proportional to the intensity within quite wide limits. Lubimenko and Forchel (*cf.* 291) found that the amount of chlorophyll per unit of fresh weight decreased with illumination, while the size of the chloroplasts increased. Holman (205) observed destructive effects of bright light upon the green pigment in living leaves of *Phaseolus.* The relative chlorophyll content differs widely among different plants and along with this variation go differences in the rate of assimilation. According to Lundegardh (291) facultative shade plants seem to possess greater plasticity with respect to chlorophyll concentration than do obligate shade plants. For example, at low intensities, chlorophyll increases with rising light values less rapidly in *Picea* than in *Pinus.* Chloroplasts of shade plants usually are larger and contain a lesser concentration of green pigment than sun plants (308). Shade plants are able to use efficiently small amounts of light and their respiration rates are relatively lower (155) than typical sun plants. Lundegardh (191) has shown that photosynthesis in shade leaves falls off at about one-tenth the intensity of ordinary sunlight, while in sun leaves CO_2 assimilation may proceed at an increasing rate at five times this intensity. In view of the findings of Emerson (118) and Fleischer (128) that the rate of photosynthesis varies with the concentration of chlorophyll, it may be seen that the quantity of this pigment is extremely important in the economy of green plants.

Several recent papers are of interest in regard to effectiveness of different wave lengths in formation of chlorophyll. Sayre (456) grew seedlings of corn, wheat, oats, sunflower, radish, mustard

and bean under Corning glass filters and observed the progress of pigment formation. Wave lengths longer than 680 mμ were not effective in the development of chlorophyll but all other regions of the solar spectrum down to 300 mμ were effective, provided the energy value was sufficiently great. For equal energy values, the effectiveness increased with the wave length to about 680 mμ and then ended abruptly. However, Shirley (490) found that plants grown under a blue glass, transmitting wave lengths between 374 and 585 mμ at 10 per cent of the total daylight intensity, often gave a greater concentration of chlorophyll than any other regions of the solar spectrum at the same intensity. The chlorophyll concentration was usually lower under a glass which transmitted only rays longer than 529 mμ. Colla (82) found that chlorophyll was formed upon exposure of etiolated plants to ultra-violet in the region 330–390 mμ at an intensity too low for starch formation. Rudolph (447) studied formation of chlorophyll in seedlings of the wax bean grown in darkness and exposed to light for brief intervals, and reported that efficiency for pigment production was proportional to the wave length in the visible spectrum. Meier (315) found that chlorophyll was formed best in algae when the blue-violet region was included in the incident radiation. Guthrie (176) found that the amount of chlorophyll could be diminished by growing plants in continuous light or by removing the blue region from the solar spectrum, and suggested that the red radiation may be injurious when the blue-violet is deficient. Stephan (520) and Johnston (227) both have suggested that high proportions of infra-red radiation may be harmful to the chlorophyll mechanism. The recent paper by Hubert (212) is of interest from the standpoint of chlorophyll decomposition by light, which occurs readily in solution outside the plant.

A few contributions have been made concerning the influence of the daily light period upon chlorophyll development. Some of Garner and Allard's (146) observations are of interest in this connection. Under only 5 hours daily light exposure, sweet potato, soy bean, Irish potato and turnip became etiolated but peanut and *Aster linarifolius* retained their green color. A somewhat longer day but still too short for flower production, caused a deeper shade of green than normal. Poinsettia grown in short days developed the usual red bracts but when transferred to long days vegetative

development was renewed and the red color of the bracts changed to green. Arthur (10) noted that certain plants, particularly tomatoes, were not capable of maintaining their green color under long daily exposures to artificial light. Chailakhian (73) studied chlorophyll development in *Panicum, Soja, Triticum* and *Pisum* growing under short and long day conditions. Early in the life of the plants, longer days appeared more favorable for chlorophyll development but later, after 3–4 weeks, the shorter day favored pigmentation. Chailakhian supposed that the accumulation and content of chlorophyll in plants growing under natural conditions increases under the influence of the day length and interprets data of Lubimenko for several hundred plants in support of the theory that chlorophyll concentration increases as the distance from the equator decreases.

Considerable interest has been shown in recent years in the phenomenon of albinism in higher plants, especially from the genetic viewpoint. Lebedeff (270) found no difference in the phototropic response nor in the development and growth energy of the leaves of albino and green maize seedlings, and concluded that the physiological determinants were not linked with those for the chlorophyll apparatus. Pollacci (399) claimed that partial albinism in "Mentana" wheat may be overcome by placing the plants in well lighted conditions. Ultra-violet light, even for very short periods, was said to "cure" albinism. Similarly variegated leaves of *Arundo Donax* var. *foliis variegatis* were claimed to lose their albinism when placed in very bright light.

It is usually stated in textbooks that chlorophyll is never found in roots with the exception of certain aerial roots of orchids, but what this fundamental difference is between the root and shoot has not been ascertained. However, chlorophyll has been reported in the roots of barley and several other plants exposed to light (154, 496). Gautheret (154) reported more rapid formation of chlorophyll in barley and *Ipomea purpurea* roots exposed to light when the roots were excised from the plant and supplied with sugar in a culture solution. Powell (405) has reported that in 13 out of 16 species studied, chlorophyll was formed in the roots which were exposed to light.

Reflection of light from the green leaf surface has been measured by Shull (495), and the light absorption of green leaves has been

determined by Willstätter, Tswett, Herlitzka (*cf.* 514), Schanderl and Kaempfert (464), and others. Spohn (515) determined the transmission and reflection of autumn colored leaves. Recently, Seybold (485) reported upon optical properties of albino and normal leaves in a series of articles, showing that in the green leaf about 50 per cent of the incident infra-red is absorbed and about 90 per cent of the solar ultra-violet, while maximum visible light absorption occurs in the long red region at about 670 mμ. The infra-red absorption spectra of chlorophyll and several other plant pigments have been studied by Starr (516) and the ultra-violet absorption of chlorophyll has been measured by several investigators (275, 100). Lewkowitch (275) found that an alcoholic solution of chlorophyll possessed absorption maxima at 420 mμ and 325 mμ. For further information on green pigments of plants the discussions by Lubimenko (283), Dubosc (108), Stiles (526), Spoehr (514), Schertz (468), etc., are helpful.

OTHER PIGMENTS

In addition to its action upon chlorophyll, light exerts its influence upon plants through other pigments, as mentioned before. In leaves and fruits of green plants, the yellow-red carotin and xanthophyll are commonly associated with and masked by chlorophyll, while the common red and purple colors of flowers, fruits, etc., are usually due to anthocyanin pigments present in the cell sap. Autumnal coloration of leaves comes about by fading of the chlorophyll, which then unmasks the associated pigments (455). Smith and Smith (506) tied black bags around growing tomato fruits and found that no chlorophyll developed in total darkness, but the white fruits gradually changed color to yellow or red (due to lycopin, an isomer of carotin) as they matured. Veselkine and others (558) found that tomato fruits enclosed in black bags remained white with only small amounts of lycopin inside the fruits. Several varieties developed a lower carotinoid content in darkness. Murneek (346) found that when *Cosmos, Salvia* and *Soja* were exposed to different photoperiods there were marked differences in the time of sexual development, and that the carotin and xanthophyll increased in plants which had changed from the vegetative to the reproductive state. Rudolph (447) has shown that carotin and xanthophyll are formed less rapidly in red than in blue light.

Norris (366) observed the development of chlorophyll and carotinoid pigments in etiolated plants following irradiation with a 200 watt tungsten lamp for 51 hours. Chlorophyll and xanthophyll increased in a constant ratio but carotin decreased at first and later developed more rapidly than the other two pigments. Euler and Hellstrom (120) found a constant chlorophyll/carotin ratio in etiolated barley seedlings when exposed to light, while the chlorophyll/xanthophyll relationship increased with the age of the seedlings. MacKinney (295) also observed a constant chlorophyll/carotin ratio, which may be taken as further evidence for the interrelationship of these pigments in photosynthesis (*cf.* 19). In a recent book citing 201 references, Lederer (271) has described the properties of carotinoids at length and has concluded that their use to the plant is not yet definitely known.

Formation of anthocyanin pigments under controlled light condition has been studied by Adams (2) who grew several kinds of plants under continuous artificial light supplied by a 700 watt Mazda lamp, and reported normal coloration of flowers as follows: white in wax bean, yellow in tulip, blue in hyacinth, red in the stamens of castor oil bean. Kosaka (251) found that only in the presence of light was the natural pigment formed in the flowers of *Chrysanthemum* and, furthermore, that low temperatures (7–15° C.) favored, while higher temperatures (25–30° C.) inhibited, pigmentation. Kuilman (259) found that a chromogen was produced by a photochemical reaction whose rate was not influenced by temperature. This chromogen was changed to anthocyanin by a dark reaction which was affected by temperature. Mirande (325) described the formation of purple anthocyanin in lily bulb scales under the influence of blue-violet and, to a lesser extent, the red portions of sunlight. This same author (326) found a correlation between oxidase activity and the presence of anthocyanin, as was later found also by Onslow (370). McCrea (312) found that a red pigment developed in the mycelium of *Claviceps purpurea* when exposed to short light rays. Much interesting experimental work has been done recently upon coloration of apples by radiation. Magness (299) found that Jonathan apples were colored by ultraviolet radiation. Fletcher (129) observed that apples bagged in red cellophane on the tree failed to develop the red pigment. Later Pearce and Streeter (276), Arthur (9) and Freytag (137) re-

ported, as a result of careful experiments, that development of red pigmentation in apples is brought about by the blue-violet and the ultra-violet of sunlight. There is considerable evidence indicating that a relatively high sugar content may favor formation of anthocyanin in leaves (172, *cf.* 168).

Since carotinoids show characteristic absorption bands, it is possible that the absorbed energy of certain wave lengths may be converted to chemical use. Other theories have been suggested, *e.g.*, that perhaps these pigments may be concerned with oxygen transference, or that they may control the equilibrium between chlorophyll *a* and chlorophyll *b* (*cf.* 168). Many natural pigments, including glucosides, anthracines, anthraquinones, etc., are known to fluoresce, but little is known about their uses to the plant. Petri and de Cecco (389) have studied fluorescence in 164 species of plants. Anthocyanin pigments have characteristic absorption bands, one in the middle of the visible spectrum at about λ 500 mμ and another in the ultra-violet (475), the exact position depending upon the nature of the pigment and its solvent (442). Schmucker (472) has studied quantum relations in photosynthesis of green tissues with and without accessory pigments present in the cells, and has found that due to their absorption of the incident light, carotinoids decreased the effectiveness of the blue region by 15 per cent. The presence of flavone and anthocyanin in alpine plants has been ascribed to the action of intense light, particularly the shorter wave lengths, and it has been suggested that these pigments may exercise a protective rôle by screening out the light from deeper lying cells (*cf.* 402). Rosenheim (446) found that less flavone developed in *Edelweiss* when grown at lower altitudes than when grown on the Alps. For further information on plant pigments, the works of Onslow (370), including 879 reference, and Mobius (327), including 300 references, and those of Palmer (379), Gortner (168), Karrer and Helfenstein (232) and others (257, 258) may be consulted.

CHROMATIC ADAPTATION

The matter of chromatic adaptation, described by Gaidukov in 1904 (*cf.* 291), has been of considerable interest in connection with attempts to account for zonal distribution of aquatic algae. Wurmser (*cf.* 291) reported that red algae in green light assimilate more

rapidly than green algae under the same conditions, and similar conclusions have since been reached by other workers (333, 552). Harder (184) found that blue races of *Phormidium faveolarum* have their maximum assimilation in red light, while red races assimilate best in blue light. Boresch (43) found that out of 18 species investigated, only four developed a coloration complementary to that of the colored light under which they were grown experimentally. In the complementarily colored species of *Phormidium* and *Microchaete,* red light favored development of blue phycocyanin and green light enhanced formation of the red phycoerythrin. The quality and intensity of light available for submerged water plants vary with depth, color and turbidity of the water (492). Lundegardh (291, 492) states that the matter of adaptation to conditions of low intensity and relatively greater proportions of blue wave lengths in deep water may be determined by either a low compensation point or by absorption and use of complementary radiation. Not only the quality of light but also its intensity is important in maintenance of a favorable CO_2 balance in the variously pigmented groups of plants. Higher intensities of light are required by green and brown algae than by red algae (552, 330). Lubimenko and Tikhovskaiia (288) are of the opinion that the light spectrum and color of plant plastids are of no primary importance for distribution of marine algae at a depth of 50 meters. Recent papers by Montfort (331) and Seybold (487) show that adaptation of marine species to intensity and wave lengths of light has an influence upon physiological functions. The ability of red algae to absorb a large percentage of blue light explains, in part, their ability to live in relatively deep water.

The relative effectiveness of different regions of the solar spectrum for carbohydrate synthesis is strongly reflected by the ability of plants to grow successfully. The function of wave length in the growth of many different kinds of algae has been studied by Teodoresco (534), Meier (315) and others, and in general it has been found that green forms thrive best when grown under red light in the region of the red absorption band of chlorophyll, though some other groups possessing considerable proportions of other pigments (as the diatoms) may be able to use blue-violet rays to relatively better advantage than can the grass-green algae (534). Purple bacteria can synthesize carbohydrates in darkness, but the rate of

carbohydrate formation is more rapid in the presence of light (556, 443). Green bacterial pigments are, in many respects, similar to the chlorophylls (473). Recent work indicates that absorption of light by the purple pigment has no significance for carbon dioxide assimilation in bacteria (443).

PHOTODYNAMIC ACTION

The importance of light-absorbing materials in plants may be emphasized by brief reference to the photodynamic action of dyes which have been experimentally introduced into living tissues. Many years ago Hertel (197) found that ultra-violet radiation of 280 mμ killed bacteria, while under normal conditions blue and green wave lengths were without effect in this respect. In the presence of dilute eosin, bacteria were killed by green light in the region of the absorption band of eosin, but remained unharmed in blue light which was absorbed, neither by the dye nor by the bacterial cells. The eosin apparently acted as an optical sensitizer much as does chlorophyll which has a very powerful "photodynamic action." Explanation of photic sensitization in plants appears to be similar to the case of the photographic plate. The absorbed dye acts as a light absorbent, and the effect seems to be produced by activation of oxygen or by the oxidized dye product, since oxygen must be present for the phenomena to take place.

The addition of very small amounts of fluorescein dyes to yeast cultures has been found to have little or no effect upon growth of the yeast cells in darkness, but in the presence of light, growth is checked (296). Navez and Rubenstein (324) obtained an increased rate of starch hydrolysis by diastase upon the addition of dyes of the fluorescein series in the presence of light. A very interesting example of photosensitization in relation to growth has been demonstrated by Blum and Scott (38) with wheat roots grown in nutrient solution. After the addition of 1 : 500,000 erythrosin to nutrient cultures in glass vessels, unilaterally illuminated roots exhibited relatively greater growth rates on the shaded side so that bending occurred toward the light, whereas without the dye these roots were not phototropic. This response was attributed to light-absorption by the dye in a manner similar to that exhibited by the naturally occurring porphyrins in plants which are generally photodynamic.

A photosensitive effect of eosin upon growth of *Vicia faba* roots has been reported by Prescher (406). With appropriate dilute concentrations of dye, root growth and mitosis were hindered by light. Also, Becker (according to Prescher) has found that methylene (1 : 100,000) is capable of causing abnormal nuclear divisions in direct sunlight but not in darkness. Furthermore, the effect of strong artificial light in overcoming dormancy of seeds and winter buds of woody plants is known to be enhanced by the presence of dilute photocatalysers, *e.g.*, eosin, methylene blue, erythrosin, etc. (355). All this evidence suggests that in the normal course of events, where light exerts an action upon growth, it probably is brought about by absorbing substances (pigments) naturally present in the plant.

Many other examples of optical sensitization are on record in both plants and animals (265, 482). A striking example of photochemical action is the photolysis of red blood cells, where the relative hemolysing efficiency of the solar spectrum coincides with absorption curves of oxyhemoglobin (274). Experiments of Jirovec and Vacha (225) with green and colorless forms of *Euglena gracilis* suggest that oxygen may be contributed to light sensitive reactions through the action of light upon the chlorophyll-photosynthetic process. Ingestion or injection of certain plant materials are known to render animals sensitive to light (265, 318). An extensive review of the general subject may be found in Blum's (37) paper on "Photodynamic Action."

TRANSPIRATION

Loss of water from aerial portions of plants has been given much attention by physiologists. Along with several other factors, intensity of radiation has been found to be of great importance in controlling rate of evaporation from the shoot and, hence, rate of water absorption by the roots (13, 457). Martin (303) has found a linear relationship between transpiration rate in *Helianthus* and light intensity. Depending upon the evaporating power of the air, the fraction of transpiration due to direct effect of radiation varied from 38 to 81 per cent. Other workers have found that water content of plant tissue is lowered and organic matter increased proportional to the square root of light intensity, as the latter is increased over a considerable range (269). The rôle of light in

regulating stomatal apertures through which a large proportion of the evaporation takes place appears to be controlled by variation in the hydrogen-ion concentration of the guard cells which in turn controls their turgor (459). Redington (430) has observed that rapid transpiration may set up a tension on the sap so that water is withdrawn from the differentiating tissue below the meristems. A number of species, such as *Pelargonium, Humulus, Boehmeria,* etc., when grown under continuous light conditions, exhibited cyclic reduction in leaf area by abscission which was followed immediately by decreased transpiration and increased growth of the stem. It would appear that a method of protection against excessive drying out has been adopted (perhaps fortuitously) by plants. When moisture supply becomes low, the stomata may close even in the light to the extent that both photosynthesis and transpiration may be decreased (76, 474, *cf.* 492, 48).

Transpiration from tobacco plants in relation to radiant energy in visible and ultra-violet radiation was studied by Arthur and Stewart (13) with temperature and humidity controlled by standard air-conditioning machinery. Within a temperature range of 73°–78° F. the rate of water loss due to visible light greatly exceeded that occasioned by infra-red energy, but at high temperatures of 98°–100° F. the infra-red rate of water loss increased so rapidly that it almost equalled the visible rate. Since the stomata were closed under the infra-red, it is believed that the high rate of transpiration must have been wholly cuticular. It was concluded that transpiration from leaves under high radiation values at high temperatures probably places considerable tension on the water system and thereby diminishes growth rate. That growth is dependent upon a liberal supply of water has been emphasized in the recent work of Loomis (282) where it was found that sunlight and soil and air moisture are important factors contributing to the maintenance of turgor and growth in maize.

ABSORPTION AND USE OF SOLUTES

Effects of light in relation to adequate supply of water and nourishing materials to growing regions of plants have received considerable emphasis. Priestley (407) made a special study of morphological and structural features of etiolation in legume seedlings grown in complete darkness. Peculiar suppression of foliar or-

gans, abnormal elongation of the stem and development of a plumular hook were correlated with decrease in superficial cuticle formation and accumulation of fatty and proteinaceous materials in the cell walls of the region intervening between the meristem and the vascular supply. The main features of etiolation were regarded as consequences of altered permeability and decreased diffusion of dissolved food substances to meristematic cells. The author concluded that brief daily exposures to light accelerated migration of these impregnating substances to the surface of the plant and thus increased the aqueous nutrient supply to the apical meristem.

It is not yet sufficiently clear as to how light affects the availability of essential nutrients through modifications of solute absorption, but several contributions may be mentioned. Redington (429) reported that no quantitative relationship existed between the amounts of water and salts absorbed since maize and barley grown in continuous light showed relatively low ash content as compared with the same kinds of plants grown under intermittent light. Scott and Priestley (410) have pointed out that the processes by which water enters the plant are quite distinct from those by which salts enter. Nemec and Gracanin (351, 352) reported that relatively more K was assimilated by barley in violet and red light than in green, while Weissman (587) found that the percent of N, phosphoric acid and K was greater in shade grown barley, rye and wheat than in sun grown plants of the same species. Hoagland, Hibbard, and Davis (202, 203) found that the rate of absorption of certain ions was influenced by light, the uptake of bromine and chlorine by illuminated *Nitella* cells being considerably increased over that of control plants kept in darkness. Concentration of bromine in the cell sap was proportional to the number of hours of daily illumination. Gracanin (169) grew barley in phosphate solutions placed in thermos bottles (to shield the roots from change in temperature) and reported that no differential effect upon P absorption could be shown when the shoots were illuminated or kept in darkness.

In an interesting paper on oxygen relations of plants, Cannon (66) has shown that under certain conditions the partial pressure of O_2 in the stem and probably also in the root increased when

plants were placed in sunlight, which is in accordance with expectations.

Hibbard and Grigsby (198) have studied the effect of Ca and K deficiency along with different daily light exposures upon the growth of *Pisum sativum*. It was found that the light quality and period of illumination had greater effect on the type and quality of growth than did differential salt solutions of K and Ca deficiencies. Absorption of K and Ca was found to be more rapid in the light. Using a full nutrient solution, the dry weight of shoots grown in short daily light periods was about 22 per cent less than that of plants grown in continuous light. However, with calcium deficiency this difference was decreased to about a 2 per cent difference between short day and continuous light regimes. In this connection, the results of Panchard (380) with *Raphanus sativus*, grown to maturity under high and low light intensities, are of interest. It was found that under low light conditions organic synthesis was greatly limited toward maturity while the intake of ash constituents continued, so that the actual per cent of ash content in relation to organic weight was much higher under restricted lighting.

That light, particularly short wave lengths, influences absorption of inorganic nitrogen has been reported by Tottingham and others (547, 548). Absorption of nitrate per gram dry weight of tissue in wheat plants was said to be increased by blue to longer ultra-violet radiation from a carbon arc, when other factors were kept constant. Tottingham, Stephens and Lease (548) tested the effect of ultra-violet upon the absorption of nitrate by growing young wheat plants under Mazda lamps alone, and with added ultra-violet energy supplied by a mercury arc. Both with single nitrates and with a complete nutrient solution, response to increase in the proportion of blue to ultra-violet energy was evidenced by increased nitrate absorption. In another recent paper (546) it has been reported that blue-violet light increased the percentage of protein in the young wheat plant, while pentosans and crude fiber were decreased. Solar ultra-violet radiation was believed to increase the per cent of lipides and of uronic acids. It is difficult to say whether or not all other factors which might have accounted for the observed results were eliminated. Nightingale (359) found that tomatoes, grown in solution without nitrogen,

increased the absolute amount of nitrogen present in the plants, and that a short photoperiod was more favorable than a long one for this increase, even though less distilled water was added to the plants in the short light period.

Nitrogen deficiency is decidedly a limiting factor for growth of the vegetative parts of plants, both directly through its unvailability for the building of protoplasm, chlorophyll, etc., and indirectly through the effect upon CO_2 assimilation, which is reduced by lack of ample supplies of nitrogen (339). Gile (159) has shown that corn plants grown in nutrient solutions with nitrogen were able to take up in darkness all the nitrogen necessary for growth. If short wave lengths of visible and near visible radiation do increase absorption of certain solutes, the value of this increased uptake for the plant's welfare remains to be proven.

PERMEABILITY

The effects of light upon cell membrane permeability have been investigated by Lepeschkin (272, 273) using as a criterion the rate of dye penetration into the leaf cells of *Elodea.* It was found that greater absorption takes place in light of moderate intensity than in darkness "due to the change of permeability of the protoplasm." This increase in absorption can be localized in the illuminated part of a leaf and reaches a maximum increase in about 10 per cent full sunlight. The rays most active in producing the effect were those with a wave length of 320–420 mμ, *i.e.,* ultra-violet; less active are the violet, blue, green; least active are the red rays. These results correspond in general with the data of Brooks (57) who found that the amount of 2, – 6, dibromo-phenol indophenol penetrating the sap of *Valonia* increased as the wave length decreased. The force of attraction of protoplasm for water has been reported as being decreased by shorter wave lengths of light (329). In a study of the effect of light upon the permeability of *Paramecium* to NH_4OH, Packard (377) found that light exposure increased the permeability. The effectiveness was greater in shorter rays and increased with the duration of the exposure. Permeability of the cells of the *Avena* coleoptile was increased by light in experiments of Brauner (53). Hoffman (204) observed a great effect of light upon the penetration of glycerine into the cells of *Spirogyra.* In contrast with these results, Zycha (600) re-

ported no effect of light upon the permeability of leaf cells exposed to KNO_3 and NaCl. The plasmolysis time for KCl and $CaCl_2$ with mesophyll cells of *Ranunculus ficaria* has been shown to be short in the dark and long in the light (573). Furthermore, the permeability for sugars in parenchymatous tissues of *Daucus carota* has been shown to decrease by as much as 38 per cent in the light (55). The significance of permeability variations brought about by light has exceedingly interesting implications for the theory of growth-hormone activity.

PROTOPLASMIC MOVEMENT

Initiation of protoplasmic streaming in dark adapted cells of *Vallisneria* has been found to be most rapid in red light, less in blue and least in green rays, while infra-red appears to be inactive (480). If protomplasmic streaming is influential in the translocation of solutes (*cf.* 89), then light certainly must be a factor in the movement of materials in plants. Fitting (127) found also that red rays were most stimulating in causing resumption of streaming in dark adapted cells of *Vallisneria*. Others have found, likewise, that suitable intensities of different wave lengths of visible radiation stimulate protoplasmic movement (23), but that the effect may be retarding or stimulating, depending upon intensity as well as upon wave length (49).

Orientation of chloroplasts under different light conditions is of interest because of the relation of this phenomenon to efficiency of CO_2 assimilation. Gistl (161) observed that plastids of *Schistostega* collected on the more intensively illuminated part of the inner wall of the lenticular cells of the protonemata. Voerkel's (562) observations concerning relative effectiveness of different regions of the spectrum in relation to phototaxis of *Funaria* chloroplasts, show that within the range of intensities employed, the blue, blue-green and yellow-green rays induce the chloroplasts to assume a position next the outer cell wall in a plane so as to expose their optimum surface to the incident light. In red light and in darkness the plastids become arranged along the sides of the cell walls.

ASSIMILATION

Any discussion of the chemical constitution of plants in relation to their growth and differentiation would turn naturally to a con-

sideration of fundamental materials, such as carbohydrates, nitrogen and other essential constituents. The dry weight increase of plants is intimately associated with their rates of photosynthesis, and increase in growth rate with increasing light intensity has been found up to 50 or 100 per cent of ordinary sunlight (490).

For optimum growth of any green plant under a given set of conditions with respect to temperature, mineral nutrition, water supply, etc., there is a certain light exposure of optimum intensity, quality and duration. The quantitative relationships between

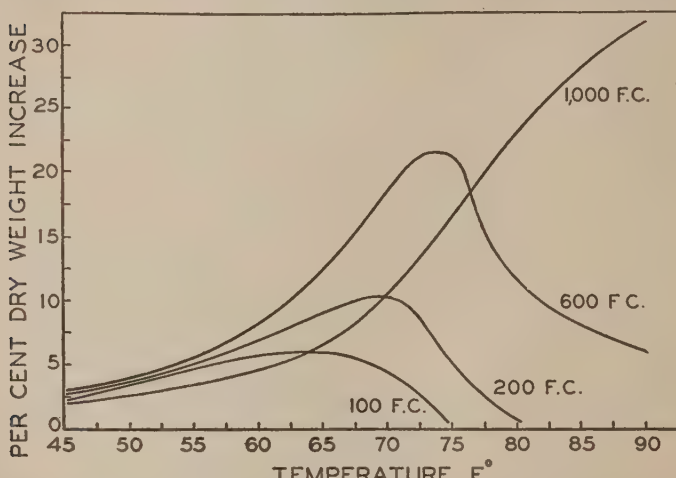

FIGURE b. The assimilation rate in young tomato plants in relation to light and temperature. Under a low light intensity of 100 foot candles, the relative increase in dry weight reached a maximum rate at about 65° F. With increasing intensity, the maximum was shifted toward the higher temperatures. Under bright light of 1000 foot candles, even a high temperature of 90° F. was favorable for assimilation. After Bolas (40).

radiation and temperature and plant growth have been worked out in an interesting fashion by Bolas (40) in experiments with the tomato. Separate groups of plants were grown in glass houses under several different light intensities varying up to 1000 f. c. For each intensity there were also several different temperature values ranging from 45° F. to 90° F. The per cent increase in dry weight in a 7-hour period showed an optimum value at higher light intensities as the temperature increased. At 60° F., assimila-

tion reached a maximum at about 100 f. c. light intensity, and decreased markedly with increased intensities at the same temperature. However, at 85° F. assimilation increased with increasing light intensity up to a maximum near 1000 f. c.

Gilbert (157) investigated the effect of different day lengths and temperatures on the growth of six species of plants. Specimens of *Xanthium pennsylvanicum* were grown in 11 hours and 14 hours of light daily, both in high temperatures (60–90° F.) and low temperatures (40–70° F.). Under both temperature conditions the longer daily exposures permitted much longer periods of vegetative growth and greater final height before reproductive processes terminated the experiment. The greatest vegetative development occurred under long day and low temperature conditions, and the author concluded that the action of the light period on the plant is modified by humidity, nutrient supply, and temperature in accordance with Blackman's theory (modified perhaps, *cf.* 222) of limiting factors; the latter states that the pace of a process is set by the factor in minimum (33). Eaton (109) found that soy beans exposed to a day length of 13 hours and subjected to different temperatures at night, *e.g.,* 90°, 65° and 50° F., gave the greatest average height and total dry weight at the lowest temperature.

For the building of protoplasm, protein synthesis is of prime importance, and experimental evidence indicates that all living cells have the ability to form protein, provided that supplies of carbohydrates and suitable nitrogenous compounds and other essential constituents are available. That light is not directly essential to this process has been demonstrated conclusively (338, 111, 361). Indirect effects of light upon the processes leading to protoplasmic synthesis are important nevertheless, not alone through the supply of carbohydrates by photosynthesis (360, 362) but also through increased uptake of nitrate from the nutrient solution during exposure to shorter wave lengths of solar radiation (547).

There is also some evidence to show that the quantitative use which plants can make of carbohydrates and inorganic nitrogen may be controlled by daily light exposure (359, 546). If light is insufficient for rapid synthesis of carbohydrate foods, nitrogen cannot be used effectively (409). Under certain conditions proteins are respired as the source of energy (362), especially when

carbohydrates and fats are diminished by conditions unfavorable for photosynthesis. Kishi and Yokota (238) have observed that proteins were decomposed when mulberry plants were shaded.

The total and relative proportions of the different kinds of carbohydrates occurring in plants have been studied in relation to light environment by Garner, Bacon and Allard (150), Deats (96), Hurd-Karrer (216), Arthur, Guthrie, and Newell (12), and many others. Garner, Bacon and Allard (150) found that elongation of the stem of summer radish resulting from long daily exposures to light was associated with an increased content of reducing sugars, particularly in the upper portion of the stem. Changes in the form of carbohydrate content and in the degree of hydration of the plant tissues were among the earliest observable effects of change in the length of day to which plants were exposed. Transfer of *Cosmos* from a long to a short day resulted in material increase in reducing sugar in the upper portion of the stem within 48 hours after the transfer had been made. Two days later the increase in sugar content was in the form of polysaccharide accompanied by a slight decrease in the water content of the plant. Twelve days later the increased content of sugar was again in the form of monosaccharide, flower buds had appeared and the water content of the tissues had increased. In Biloxi soy bean exposed to natural length of day in late summer a slight increase in reducing sugar was found in the leaves at about the time of flower bud formation, followed by a decrease at the time open blossoms appeared. A marked increase in reducing sugar and a small increase in soluble nitrogen was observed 15 days later during rapid development of the fruit.

Deats (96) found that cell sap concentration in the leaves was greatest in plants exposed to a long day, but it was more concentrated in the fruit of tomato which had grown in a short day. Hurd-Karrer (216) found that in young wheat plants the glucose, total sugar, acid-hydrolyzable material and total carbohydrate increased under long day conditions. Glucose content of the culms was 2 to 3 times that found in the leaves, though there was little difference in the pH of culm and leaf. Other investigations have shown that interception of sunlight may bring about increase in the per cent of water and of non-protein nitrogen, and decrease in the per cent of dry matter, the pH and the soluble carbohydrate

(238). Nitrogen fixation by symbiotic bacteria in soy beans is known to be enhanced by regulating light intensity to a value which gives a suitable carbohydrate content (371).

Arthur, Guthrie and Newell (12) have shown that various values for the carbohydrate fractions may be obtained, depending upon when plants are sampled in relation to their light exposure period. In radish the total carbohydrate varied from 7.49 to 34.73 per cent among plants which showed flowering response, while a range of 8.95 to 21.23 per cent was found for those which did not flower. Flowering was initiated by illuminating the plants for 8 hours each night with 170 f. c. without any resultant accumulation of carbohydrates. By using an intensity of 700 f. c. for 6 hours each night, flowering was induced as well as an accumulation of carbohydrates. Also nitrogen supply over a considerable range was controlled in sand cultures without effect upon the flowering stage. The authors concluded that in radish (and also in other plants), flowering was quite independent of carbohydrate-nitrogen relations and depended only upon day length. It was also shown that the per cent of simple carbohydrates in cabbage was doubled on a 19 hour day as compared to a 5 hour day.

CARBOHYDRATE/NITROGEN RATIO

In the past few years, considerable attention has been given to the relative proportion of carbohydrates and nitrogenous compounds in plants and their influence upon various developmental phenomena. In 1916 Fisher (126) reported that the vegetative condition in plants is characterized by a low carbohydrate/nitrogen ratio, while the reproductive stage is characterized by a high ratio of these constituents. Kraus and Kraybill (234) investigated vegetative growth and reproduction in the tomato in relation to available carbohydrate and nitrogen supplies, and found that the ratio of carbohydrates to nitrogen was an important determining factor for growth and differentiation. Four different conditions of C/N and the associated developmental characteristics were described: (1) With an abundance of water and nitrogen and low carbohydrate supply, the plant was weakly vegetative and nonfruitful. (2) With little nitrogen and abundant carbohydrate both vegetation and fruitfulness were suppressed. (3) With abundant nitrogen and medium carbohydrate supply, vigorous vegetative

growth ensued but the plant remained sterile. (4) Starting from conditions favorable for vegetative growth, a decrease in nitrogen with a slight increase in the carbohydrate reserve, caused less vigorous growth and induced fruitfulness. Investigations of Klebs (240, 241) concerning effects of light intensity, temperature and soil nutrients in the development of *Sempervivum,* pointed to the same general conclusion, *i.e.,* that not the absolute values but the relationship between the several factors is of consequence. Klebs found that vegetation and reproduction could be controlled by altering the environment in a suitable manner. Plants ready to flower could be reversed back to the vegetative condition and caused to form vegetative rosettes on the elongated axes by reducing the light, keeping the temperature at about 26° C. and supplying plenty of fertilizer. Very strong light caused flowering without formation of an elongated axis.

Many other investigations have since given support to this general principle of C/N balance (358, 359, 362). Miss Hicks (200) followed the distribution of carbon and nitrogen in different organs of the wheat plant through different periods of its life history, and reported that successive stages of development are initiated by critical values of the carbon/nitrogen ratio, that this ratio increased throughout the vegetative period and, when sufficiently high, flowering occurred. A low ratio of carbohydrates/nitrogenous materials appeared to be characteristic of growing points. Conditions favorable for flower initiation may not be favorable for fruit formation (362) because, following fertilization, the young fruit acquires the chemical character of a growing point (200, 342) and absorbs proportionately greater amounts of nitrogen (*cf.* 210). That a high C/N ratio favors initiation of roots in cuttings was pointed out by Reid (433, 434, 410, 438). Also Schrader (476) found that relatively greater proportions of carbohydrates favored rooting in tomato cuttings. Furthermore, it has been found that when cuttings of *Salix viminalis* are planted, shoots grow from the area of lowest C/N ratio and roots from the regions relatively higher in carbohydrates (199). The interrelationship of carbon and nitrogen in growth of germinating seeds with different kinds of stored food has been worked out with great care (435, 436, 437).

As Kraus (253) has pointed out, the changed or changing morphological expression is the external evidence of changed or

changing chemical composition. The same author has emphasized that the conditions which determine meristematic differentiation are quite different from those accompanying further development of the various parts in question. The conditions for flowering may not be those for fruit setting and development. Nitrogen is not all-important as a factor in the growth/differentiation balance but other stuffs, such as sulphur, phosphorus, potassium, etc., the water supply, light and temperature are all significant.

The discovery of photoperiodism came at about the same time as did the announcement of the C/N principle, and in the years immediately following, numerous efforts were made to interpret the effects of light upon plants in terms of its influence upon the relative proportions of the building materials necessary for growth and development. Nightingale (358, 359) grew many kinds of plants under long and short daily exposures to light and with varied supplies of nitrates, and obtained results which agreed in general with the C/N relations previously outlined by Kraus and Kraybill (254). An important point of distinction was found by Nightingale in *Salvia,* buckwheat, soy bean and radish grown in a short 7-hour daily light period wherein plants were not able to fully utilize their carbohydrates, apparently through inability to synthesize the supplied nitrate to other forms of nitrogen. When these high carbohydrate short-day *Salvia* plants were transferred to long day conditions, the ensuing rapid growth was accompanied by more rapid nitrate assimilation and greater accumulation of organic nitrogen. The author expressed the opinion that the significant ratio in growth is that of carbohydrate/insoluble nitrogen, since accumulated nitrate did not affect flowering. It should be pointed out that the *Salvia* plants grown during a day of 7 hours and with full daylight supplemented at night by 6 hours of weak artificial light, showed no significant differences in the per cent of carbohydrate or total nitrogen. Apparently, the additional energy of the longer days made but little contribution to the photosynthesis beyond that found in the 7-hour day. The point to be emphasized is that flowering occurred in the short daily exposures, while in the long days the reproductive stage was not attained. In forcing plants with supplementary artificial illumination, Oden (368) found that the ratio between carbohydrates and proteins increased with an increasing amount of the longer wave lengths of

light. Gilbert (157) grew *Xanthium* in long and in short days, and found that C/N ratio ascended as the plants approached maturity. Hurd-Karrer (216) observed that in young wheat plants, sampled at the age of tillering (branching from the base), the total carbohydrates were highest and the per cent of nitrogen was lowest in the leaves when the plants were grown in long day conditions which accelerated culm elongation and flowering. The lowest carbohydrate and highest nitrogen percentages were associated with a short day exposure, which retarded heading and gave large vegetative plants, with reduced yield of grain or total sterility. Correlations between the carbohydrate/nitrogen ratio and fruitfulness were found only in the analyses made on the culms, and not in those made on the leaves.

In the opinion of many investigators, the magnitude of the carbohydrate/nitrogen ratio is probably not the primary cause of the growth/differentiation balance. As a result of studies in the relation of carbohydrates and nitrogen in the flowering behavior of apple spurs, Harvey and Murneek (189, *cf.* also 209, 210) concluded that the C/N ratio is important as an indication of possible limiting situations, but that it should not be given a causal relationship in bringing about a particular formative change in the plant. Tincker (542) found that *Helianthus tuberosus,* grown in a reduced light period was unable to use all the carbohydrates for shoot growth and stored the excess food in tubers. In *Phaseolus multiflorus,* grown under short day conditions, the food was stored also in the thickened roots. A relatively high C/N ratio was correlated with earlier flowering, and the author concluded that the length of day controlled the utilization of the photosynthetic products and the rate of stem elongation, and thus influenced the C/N ratio which appeared as a result rather than as a cause of the morphogenetic trend. It is of interest in this connection to note that no difference has been found in the course of photosynthesis in millet grown under 9 and 18 hours of light daily (530). The results of Hibbard and Grigsby (198), who reported that the per cent of nitrate in *Pisum* increased in short photoperiods, appear to lend support to the theory that light exerts some control over utilization of food by the plant. Jaccard and Jagg (221) have found that plants grown under continuous light show less mean CO_2 assimilation per hour and per unit leaf area than plants grown under periodic light conditions.

Hopkins (211) grew soy beans under different lengths of day, different intensities of light and in different supplies of nitrogen. The short-day plants accumulated much starch and were also high in nitrogen, whether nitrate was added or not. In long day conditions, the plants were lower in all forms of nitrogen and in carbohydrates. Shaded plants, with and without the addition of nitrate, were generally lower in carbohydrates and higher in all forms of nitrogen than unshaded plants. The weight of nodules expressed as per cent of the total plant weight was decreased by high nitrate, short days and shading. Kraybill (256) found that shaded apple and peach trees contained more soluble and insoluble nitrogen and less sugars, starch and hydrolyzable material than unshaded trees.

Recently, Müller and Larsen (341), growing plants in N and K deficiencies over a range of light intensity, have found that nitrogen deficiency exerted a depressing effect upon the assimilation rate through some protoplasmic factor, and at high light intensity growth in area of the leaves was reduced.

Purvis (416) grew cereal plants under different day lengths and with varying nitrate supply and observed that nitrogen starvation increased the total sugar content where flowering occurred and also where it failed. Since short days which reduced the assimilating period by 40 per cent had but little effect on the sugar content, it was concluded that the effect of short days on flowering can not be exercised through concentration of sugars. Under conditions of nitrogen starvation, flower primordia appeared and flowering took place at the normal time in spite of reduced vegetative growth. An increasing amount of reducing sugars was apparent just before flower emergence in the experimental plants, but since this was preceded by flower differentiation, it was regarded as a result rather than as a cause of the onset of the reproductive phase. It was concluded, therefore, that the C/N ratio bears no causal relationship to the ability of a plant to differentiate flower initials or to produce flowers. The great range of C/N accompanying the initiation of flowering in barley and millet convinced Borodina (44) that some other immediate cause was active in the change from the vegetative to the reproductive stage. Other workers have emphasized that the accumulation of insoluble carbohydrates is a better measure of the past history of the plant than of its present or future responses (*cf.* 593, 404).

Results of thorough investigations carried out by Arthur, Guthrie and Newell (12) yield further evidence along this line. Many kinds of plants were grown under different controlled conditions of temperature, humidity, light intensity, light period and CO_2 supply. Chemical analyses were made at various times during the period of growth. Depending upon when the plants were sampled in relation to their light exposure period, various values for carbohydrate content were obtained, but the total nitrogen remained nearly constant. Tomato plants kept in darkness for 17 hours lost considerable of their sucrose and dextrose, and after about 40 hours these fractions decreased to about one third the original content. In general, percentages of carbohydrate and nitrogen could be changed by varying the light intensity, length of day, or in some plants by changing the nutrient supply in sand cultures. The range of variation of the carbohydrate and nitrogen fractions varied among the species. Over a 5 to 24 hour range of daily light exposure, *Salvia* was able to maintain a comparatively narrow fluctuation in carbohydrates and nitrogen, but under the same conditions many other plants showed large variations. The authors stated that "no relation was found between carbohydrate and nitrogen content and flowering in either long-day plants such as radish and lettuce, or in *Salvia,* a short-day plant, or in buckwheat, an everblooming type." The available information suggests that photoperiodic responses are not governed by rate of carbon assimilation, but probably are due to other photochemical reactions which can be brought about by relatively low intensities of red light, and the effects depend not so much upon the quantity of radiation as upon the actual length of the exposure period. (426).

INORGANIC ELEMENTS

The importance of certain constituents other than nitrogen and carbohydrates in light relations of plants has received attention recently. Borodina (44) observed that phosphorus deficiency delayed, while lack of nitrogen hastened, the earing stage in barley, a long-day plant. Lack of potassium under conditions of a long day (18 hours) delayed the earing stage; with a short day the plants perished without having reached this stage. Apparently the exclusion of essential nutrients from the culture solution makes itself felt more strongly with a short day. In the short-day plant,

millet, lack of phosphorus depressed the plant strongly and delayed formation of panicles, but a deficiency of nitrogen or potassium was without effect on flowering. Eidelman (113) found an increase in photosynthesis with phosphorus present, as compared with controls lacking this element, and in a later paper (114) pointed out the interrelationship between temperature, phosphorus nutrition and photoperiodic response. The presence of phosphoric acid and certain concentrations of sugar in the cell sap has been considered important in the flowering of mountain rice (278). Nemec and Gracanin (352) grew rye under colored glasses (energy not equated) and reported little difference in the phosphoric acid uptake, but found that less potassium was taken up from the culture in green, and more in violet and red light than in sunlight. Matskov(304) could find no direct correlation between intensity of photosynthesis and formation of dry matter, but ample potassium promoted the translocation of assimilated matter from leaves to roots. Potassium has been reported to have some influence also upon the development of chlorophyll and the height of plants grown in various light intensities (456).

Gassner and Goeze (152) have found that when light duration (10 hours or more) is not limiting in the life of young barley plants, a direct relationship between nitrogen supply and assimilation, transpiration and chlorophyll content (number of chloroplasts) can be demonstrated. With short days (3 hours), where light is a limiting factor, no response to nitrogen is apparent. Unlike the nitrogen effect, it was possible to demonstrate even in short days an optimum K supply below which assimilation fell off rapidly and above which it decreased gradually. Since K and N are important for their effects upon protein synthesis, it is necessary to bear in mind the influence of nutritional factors in any interpretation of the rôle of light in physiological processes.

Pfeiffer (390) studied microchemically the effect of intensity and duration of light upon calcium, magnesium, phosphate, nitrate, proteins and carbohydrates in tomato, buckwheat and four-o'clock. In all plants with short light exposures there were usually low carbohydrates and low protein reserves and in longer light periods there was an increase in carbohydrate without a proportionately increased elaboration of protein, perhaps due to a limited nitrate supply. An ample supply of nitrogen is important also for the

highest photosynthetic efficiency (340). Phosphate and magnesium were usually lower under shorter exposures, due possibly to their proportionately greater utilization in protein synthesis and tissue formation. Tincker and Darbishire (543) grew tuber-forming plants under short-day conditions, which enhanced the storage of food and potassium in underground organs. When potassium was rendered deficient, there was less translocation of dry matter into the storage organs, but the conclusion that K is necessary for translocation does not seem to be well founded (*cf.* 523). Street (493) analyzed field peas grown in nutrient solution, and reported that light exposures of 10 hours daily produced plants high in potassium and low in calcium and magnesium. However, exposures of 17 hours daily resulted in plants markedly low in potassium and usually very high in calcium and magnesium.

Investigations of etiolated plants have shown that magnesium content is decreased (27) in dark grown plants. A chemical study of expressed juice from etiolated wheat seedlings indicated that primary and secondary phosphate form the buffer action of the tissues, and asparagin appears to be the substance responsible for the peculiar inflection in the etiolation curve (214). Priestley (408) found it impossible to plasmolyze the differentiated cortical cells of plants grown completely in the dark, due to the presence of lipoidal substances causing adherence of the protoplasts to the cell walls, but after very brief daily light exposures these cells plasmolyzed readily.

Warington (571) experimented with boron deficiency in plants grown under different lengths of day, and found that boron deficiency symptoms were less pronounced under short day than under long day conditions, and also that in the absence of boron the photoperiodic responses of long and short day plants were less evident.

ACIDITY, STOMATAL MOVEMENTS, ETC.

Fluctuation of organic acids with alternating light and darkness in relation to colloidal hydration and growth has been discussed by Long (280), Tolmachov (544) and others. Eisenmenger (116) found that when actively growing tobacco plants were placed in darkness with and without a supply of nitrogen for a period of 11 days, the nitrate and amino acids accumulated

in the darkened plants. Garner, Bacon and Allard (150) investigated hydrogen-ion concentration of cell sap in different plants grown under different photoperiods. In the case of short-day plants grown under long daily periods of light, upward elongation of the vegetative stem was associated with progressive increase in active acidity, particularly in the region of the growing point which became more acid than the lower regions. Under short day exposure, the upper portions of the plant were less acid than the lower. Abrupt transfer from a long to a short day caused a sudden temporary decrease in acidity in the region of the growing point, which change was believed to indicate a transition from the vegetative to the flowering condition. Increased acidity was obtained also when the short daylight period of winter was prolonged by use of electric light of low intensity. In the case of long day plants, exposure to a short day tended to inhibit stem elongation and to keep acidity to a low level, while exposure to a long day resulted in elongation of the axis and flowering, which form of development was associated with general increase in acidity. However, there were considerable differences in distribution of active acidity in various parts of different kinds of plants. Loehwing (277) observed a diurnal pH cycle correlated with variations of light. Strong insolation depressed the sap acidity in *Triticum* to the extent of causing precipitation and ultimate unavailability of iron, leading to chlorosis.

That light brings about changes in the active acidity of the stomatal apparatus in the leaves of higher plants and in this manner influences stomatal opening has been discussed in recent botanical literature (385, 458, 459, 497, 503). Scarth (459) reported that in the presence of light acidity was lessened in the green guard cells, their turgor was increased and the stoma opened, while in darkness a reversal of the conditions took place. Pekarek's (385) experiments with vital staining in the stomata of *Rumex* supported this view. Sayre (457) has shown that the long ultra-violet and visible light is effective in stomatal movement, while the infra-red region of the solar spectrum is apparently without effect. Sierp (497) reported that the quantum theory did not apply to photic activation of stomata, the yellow, green and blue wave length regions being about equally effective in opening stomata, while red light was less effective and infra-red inactive. However,

Paetz (378) reported that stomatal movement was strongest in red light, the degree of response of the guard cells corresponding with the strength of the absorption bands of chlorophyll. Since the rate of photosynthesis follows closely the size of the stomatal aperture (155), it can be readily seen how important is the regulation of turgor in the guard cells by light and moisture supply.

PHOTOPERIODIC STIMULATION

The influence of the duration of light exposure upon vegetative growth, reproduction, food storage, etc., in plants has become a favorite topic for research since the general principles were pointed out by Garner and Allard in 1920 (145). Certain experimental data which seem relevant to the hypothesis that the light period determines outward morphological expression through some control exercised by internal physiological conditions, will be discussed at this point. Morphological aspects of photoperiodism will be treated later in connection with the phenomena of growth and reproduction.

Several interesting experiments which throw light upon the nature of photoperiodic induction have been reported by Garner and Allard (147). Different portions of the main stem of *Cosmos sulphureus* (a short-day plant) were exposed to different daily periods of illumination and, in some instances, to continuous darkness. When the upper portion was exposed to long days while the lower region received only 10 hours of light daily, the former remained vegetative while the latter flowered promptly. Conversely, flowering in the upper portion was obtained by exposure to short days, while vegetative growth continued in the lower region exposed to long daily light conditions. When the upper portion of the plant was kept in continuous darkness for a period of 3–5 weeks, and the lower portion was forced into flowering by short days, flower buds were induced in the upper darkened portion. When the lower portion was prevented from flowering by long days and the upper part was kept in continuous darkness, the latter formed no flower buds. It was concluded that darkness in itself does not initiate flowering, but also does not inhibit the formation of flower buds in response to the action of an appropriate daily light period in another part of the plant. There remains, therefore, the distinct possibility that certain materials favorable

to flower formation may be formed in one part of the plant, and thence may be transported to another part where important processes are set into action leading toward initiation of flower primordia.

The localization of photoperiodic stimulation in several tuber-forming species has been studied by Rasumov (425, 427). Stimulation of the apical growing region by short-day exposures influenced the developmental trend of the whole plant. When the upper or lower parts of the same branch were subjected to a short day, the stimulus was delayed in the upward direction but transmitted readily downward. When the apex of *Ullucus tuberosus* was darkened, the axial buds were able to grow out into long branches. These outgrowths were capable of assuming a short-day habit by induction and their developmental trend was reversed when freed from the photoperiodic influence. Recalling the action of the plant growth-substance in inhibiting development of lateral buds in *Vicia faba* (536), these experimental results of Rasumov suggest that possibly some aspects of photoperiodism are concerned with the activity of hormones. Our knowledge is as yet too meagre to permit any definite conclusions regarding the nature of the formative materials and their manner of translocation.

In the course of experiments on "photoperiodic adaptation" in Russia, several workers observed that when plants were grown for more than a certain minimum number of days during the early part of their lifetime in a given daily light exposure, and later were transformed to a different daily light period, the effect of the first photoperiod was carried over and exerted an influence upon the subsequent development of the plants (112, 103). According to Dolgushin (103), Maximov called this phenomenon the "photoperiodic after-effect." It was postulated that the accumulation of substances in the plants retards or stimulates the transition into the reproductive stage. Rasumov (423) performed experiments with millet, a short-day plant, which was grown for different lengths of time during the early stages of its life in short or in long days and then placed for the remainder of the time in long or short days, respectively. It was concluded that preliminary exposure to a certain photoperiod exerted some influence which was later manifested in the development of the plants toward maturity. Recent workers have reported that only a short-day after-effect is

possible for short-day plants, and only a long day after-effect exists for long-day plants (74). The data of Rasumov and others have been examined critically by Purvis (416) from the viewpoint of the relative efficiency of long and short daily exposures in producing flower primordia. Miss Purvis' interpretation may be summarized as follows: In the short-day type of plant, such as millet, attainment of the condition termed "ripeness to flower" (*cf.* 241) may be reached under long or short-day conditions, but five times as rapidly under short as under long-day treatment; that is, one short day is equivalent to five long days in efficiency for inducing flower formation. Though short days hasten differentiation of flower primordia, nevertheless, subsequent stages of development leading over into actual flowering are independent of day length. In the case of a long-day type of cereal, like oats or barley, the development of the condition "ripeness to flower" is less dependent on day length than in a short-day plant. In barley, differentiation of flower primordia may be accomplished in about 10 days under either long or short days, but later stages of development into mature flowering condition are considerably hastened by long days.

Lubimenko and Szeglova (287) grew long-day plants, *Hordeum vulgare* and *Sinapis nigra,* and short-day plants, *Phaseolus vulgaris* and *Soja hispida,* under different day lengths in different phases of their life cycle. They found that induction of a long day retarded development of short-day plants when permitted to continue growth under short days, and accelerated long-day plants if they were later placed under short-day treatment. When seeds were germinated and grown in darkness for 5, 8 and 10 days and then placed in long-day conditions, growth was retarded in long-day plants and accelerated in short-day plants. The authors proposed to explain the photoperiodic induction by the photochemical formation and destruction of specific stuffs which influence directly the progress of development in the whole plant and its diverse organs.

Leading suggestions on the matter of special substance and photoperiodism have come from Lysenko (293), a strong advocate of "jarovization" (*cf.* 585). This investigator states that long-day plants should really be called plants requiring continuous illumination, and that they will endure alternation of light and darkness only in case the dark period is short. Requirement for alternation

of light and darkness is inherent only in short-day plants, but this characteristic may be overcome by suitable procedures before the seeds are planted. It is claimed that by preliminary treatment (jarovization) of the seeds of short-day plants under standard conditions of moisture, temperature, darkness and light (292, *cf.* 585), both increased vegetative growth and accelerated reproductive development may be achieved even under conditions of continuous light during the growth period. The requirement for darkness, without which short-day plants such as millet cannot pass into the reproductive stage, may thus be imparted to the plant during germination (*cf.* 24). McKinney and Sando (313) found that reproduction in winter wheat was greatly accelerated by subjecting slightly germinated seed to low temperature in darkness for 50 to 65 days before sowing. Change of a winter wheat to a spring wheat by preliminary seed treatment was reported as far back as 1858 in Ohio according to these authors (313). In a discussion of some of the more important relations of plants to light and temperature, Blackman (36) has pointed out that preliminary seed treatment accelerates the onset of the reproductive phase so that during its later growth the plant is largely independent of photoperiodic conditions. Even potato tubers may be "javorized" by exposure to daylight plus supplementary light during the night at a temperature of 15° to 20° C.

Recent investigations dealing with the effect of low temperature and light conditions on seed stalk development in vegetable crops are pertinent to the present problem. Thompson (538) has given a good discussion of the induction of seeding in celery by preliminary low temperature treatment. At high temperature Miller (323) was able to maintain active vegetative growth in cabbage over a period of several years, but the same plants were forced into flower by a few months' exposure to low temperature in a cool greenhouse. Though no definite relation between sugar and nitrogen composition and subsequent behavior could be shown, there appeared to be a positive relation between the accumulation of elaborated foods in the meristematic region and seed stalk formation. Platenius (396) investigated the metabolism in vegetative and prematurely seeding celery plants at different temperatures and found that the C/N ratio varied from .5 to 14.2 in the "seeders" and from 3.1 to 7.4 in the "non-seeders." In young plants the C/N

ratio was varied over a wide range without affecting the tendency to form seed stalks, and the consistently higher ratios of C/N obtained in the later stages of development were considered as the result and not the cause of the morphological changes. Chroboczek (79) found that beets grown in a cool glass house developed seed stalks under an 8-hour light day, while in the warm house even strong continuous illumination induced seeding in only a small percentage of the plants. A combination of low temperature (50°–60° F.) and long photoperiod (15 hours or more) is the most favorable for the production of large plants and high yield of seed. Beets grown in a cool greenhouse under continuous illumination produced seed stalks in 53 days from planting, but when kept at a temperature above 60° F., even under a photoperiod of 13 to 15 hours, the plants remained in a vegetative condition for $3\frac{1}{2}$ years. Peto (388) found that high temperature favored vegetative growth while low temperature stimulated sexual reproduction in Swede turnip (*Brassica napus* var. *napobrassica*). The data obtained by Knott (243) for photoperiodic response and the facts gotten by Chroboczek (79) for morphogenetic effect of temperature, point to the meristematic tissues as being the seat of processes which determine the course of development in flowering plants. The recent attempts by Knott (245) to induce flowering in spinach by the application of localized light on the growing point, have given negative results due, no doubt, to the small area which was subjected to the light treatment.

REDUCTION/OXIDATION RATIO

The vigor and extent of vegetative growth taking place before the onset of reproduction in different species and individuals vary within wide limits, depending upon the various internal and external factors. As has been suggested upon several occasions, the relationship between income and outgo of oxidizable organic materials is a matter of considerable importance in the survival of plants under different conditions of light and temperature. Many evergreen plants appear able to assimilate carbon dioxide at a rate sufficiently rapid to maintain a favorable balance over the respiration of carbohydrates even at temperatures near freezing (585, 220). All other conditions being favorable, most plants seem capable of surviving under conditions of relatively low light inten-

sity, *i.e.*, in the range of from 1 to 5 per cent of full sunlight which approximates the light value where photosynthesis just balances respiration (the compensation point) (490, *cf.* 492). True shade plants are capable of existing for a comparatively long time under conditions unfavorable for photosynthesis. It is significant that shade-loving plants possess a relatively low respiration rate (291) in view of the fact (as Hendricks and Harvey (194) pointed out long since) that the light intensity required for the continued growth of a plant must be such that assimilation will at least overbalance loss by respiration.

Eaton (109) grew three series of each of several different species of plants in a 13-hour day and subjected them at night to temperatures of 90°, 65° and 50° F., respectively, to test the assimilation-respiration balance. Soy beans flowered earlier in high, and latest in the low temperatures, while cotton flowered earlier at the highest temperature but could make no growth at 50° F. In soy bean the greatest dry weight was formed in the cold night conditions, while the greatest final height occurred in the hothouse. Boysen-Jensen (50), from studies of the growth of light and shade plants, has shown that the quotient for maximum carbon assimilation/respiration yields a value of from 6 to 8 for sun plants and 10 to 12 for shade plants (*cf.* 486). Gabrielson (134) found the ratio for *Cucumus sativus* grown at 20° C. to be as high as 17.5, while the ratio may be still higher in other plants, *e.g.*, 25.0 in *Sinapis* (339). Lubimenko and Szeglova (286) found that the maximum dry matter per hour of light exposure was produced in a number of plants in the optimum daily periods as follows: *Gossypium*—8 hours, *Soja*—8 hours, *Sinapis*—14 hours, *Papaver*—16 hours, etc. In some plants, oxidation processes are greater in comparison with reduction processes than in other plants, and these two groups may be distinguished physiologically by the ratio of respiration/assimilation. The different daily rhythm of CO_2 exchange by different photoperiodic types of plants has been suggested as a causal factor in their response to relative length of day (440).

Great differences in respiratory rates as well as in temperature coefficients for oxidative processes are known to occur in different species (321). In some plants a carbohydrate deficit appears with a day length up to 10 hours, while in others a deficit is seen only with a day length up to 6 or even 4 hours. It is thought that these

differences are dependent upon the character of the enzymatic apparatus of the cells concerned in the processes of reduction and oxidation, (285) which control the photosynthesis/respiration ratio. Generally, increasing the light exposure to about 18 hours daily results in a corresponding increase in living substance (429). Too short periods do not permit sufficient photosynthesis of basic food, and continuous illumination appears to exert a strong inhibition upon growth through "the photochemical transformation of plastic substances" (285).

That light may have some important part in the liberation of energy by oxidative processes in living cells, has been suggested by various workers but little evidence has been offered to show direct causal relationship. Spoehr (513) noted that the respiration rate of germinating seeds was higher in sunlight than in darkness and he attributed the effect to the higher oxidative power of the atmosphere during light exposure. Parija and Saran (381) have reported recently that green and albino leaves of *Aralia,* starved for more than 40 hours in darkness and then exposed to blue-violet radiation, show increase in sugars and in rate of respiration. Red light had no effect. The explanation was offered that light increased respiration by hydrolysis of the carbohydrate reserve. Van der Paauw (375) also found an increase in respiratory rate of certain algae which were illuminated with intensities sufficiently high so as to inhibit photosynthesis. Guerrini (174) reported that red, and to a less extent the yellow, green and blue rays enhanced the rate of CO_2 evolution of *Saccharomyces cerevisiae* in a glucose solution, but these results may have been due to the temperature rather than to photochemical action. It should be mentioned here that under certain experimental conditions light is known to have a chemical influence upon respiratory enzymes in plants. In darkness, indophenol can take up carbon monoxide and become inactive. Then upon exposure to light the CO compound is dissociated to liberate the active oxidase. Cytochrome, the respiratory pigment acting as a carrier or hydrogen acceptor, is oxidized by the indophenol oxidase in accordance with the reactions worked out by Warburg and others (*cf.* 233). The reality of this light effect has been shown by the experiments of Tang (531), who found that inhibition of oxygen consumption by germinating seeds of *Lupinus albus* exposed to CO could be abolished by light. Irradiation of

the yellow ferment of yeast has yielded crystalline flavin (569), and the interrelationship of this vitamin and the enzyme has been worked out by Theorell (535).

ENZYMES

The rôle of light in relation to enzyme activity has been studied directly in vitro and also in connection with the dormancy and germination of seeds, sprouting of vegetative storage organs, etc.

Demkovskii (97) investigated the enzymes present in "jarovized" seed and found that the increase in activity of amylase, catalase and the proteolytic group proceeded at different rates. What the relationship is between the results of seed treatment and photoperiodic phenomena is not definitely known. We can suppose that the effects of temperature and light may be occasioned through the production of catalysers in the nature of enzymes, hormones, etc. Knott (244) investigated the catalase in spinach before and after lengthening the photoperiod, and found a rapid response as exhibited by an increase in the enzyme activity following a change to long days. In another paper this same author (243) reported a decrease in catalase in the apical portion of the stem of spinach and *Cosmos*, as the plants changed to a reproductive type of growth. If elongation of the floral axis ceased and vegetative growth was resumed, then a higher catalase activity was restored. Burge (61) found that *Spirogyra* exposed to light exhibited a greater catalase content than when kept in darkness. The diastase of *Aspergillus niger* was found to retain its activity in darkness and in red and green light, but the enzyme was destroyed by white and blue light according to Funke (138). Pincussen (388) observed that the destruction of diastase by light in the presence of oxygen proceeded most rapidly at the optimal reaction of the medium. Hutchinson and Ashton (218) have reported various retarding and stimulating effects upon the activity of amylase when irradiated with specific wave lengths.

It has been held by some investigators that polarized light accelerates the hydrolysis of starch (20, 298, 483, 484) in distilled water and in the living plant. The validity of these reports has been criticized by those holding opposing views (229, 428). By careful experiments, Navez and Rubenstein (348, 349) have shown that polarized light and ordinary light of the same intensity and

wave length have the same accelerating effect on starch hydrolysis when compared with controls kept in darkness. Holman (205) has described the influence of high light intensity upon the disappearance of starch from leaves which may have been due to their destruction of chlorophyll and the hydrolysis of the starch, or both.

Recently, Semmens (484) has reported the results of experiments in which a very strong beam of polarized light was made to fall upon a starch-filled hyacinth leaf. Very rapid hydrolysis of starch to sugar occurred in the light under the polarizing Nicol prism, resulting in the bursting of the guard cells, while only the usual conditions prevailed in the rest of the leaf exposed to ordinary sunlight.

Recent successful attempts to overcome dormancy of seeds and tubers have shown that resumption of growth is accompanied by increased enzyme activity (99). It has been shown, too, that several special compounds which are effective in overcoming dormancy are also capable of promoting the action of specific enzymes (80). Other workers have found that the peroxidase activity is highest in such plants as millet and barley when grown in the photoperiod which favors vegetative growth (74). The story of light in relation to enzyme activity in plants can not be told satisfactorily without further critical experimentation under well controlled conditions. The recent work carried out by Gates (153) with ultraviolet effects upon crystalline pepsin may be cited as an example of a precise type of experiment which should point the way for future investigations of enzyme photochemistry.

VITAMINS

Production of vitamins in plants has received considerable attention in recent years since the rôle of vitamins has been appreciated more fully in animal nutrition (*cf.* 559). Gunderson and Skinner (175) grew a pure culture of the alga *Chlorococcum* in a nutrient dextrose solution in complete darkness and found that vitamin *A* (or its provitamin) was synthesized in large quantities. Vitamins *B* and *G* were found also, though no *C* could be detected. Recent investigations on the synthesis of vitamin *A* in higher plants indicate that though synthesized in darkness, its formation is usually accelerated by light (30, 87, 166, *cf.* 468). Smith and Morgan (505) claim that chlorophyll is not a necessary intermediary for

the formation of carotene and lycopene or any other precursor of vitamin *A*. Fruits which develop carotene and vitamin *A* in direct sunlight, may form them also in darkness. Carotene may be considered the precursor of vitamin *A*, much as ergosterol is the precursor of vitamin *D* (334, 335). Lojkin (279) found that ultra-violet irradiated lettuce, alfalfa, spinach and soy beans (but not cabbage) developed a slight vitamin *D* content, but this method of imparting the vitamin to animals was less efficient than the direct irradiation of the animal. Clover and alfalfa hay, when cured in the sun, lose their vitamin *A* but increase their vitamin *D* content (450, 507, 508, 518). Rygh (451) found an abundance of vitamin *A* in hay which had been dried quickly. It has been shown that light acts directly or indirectly on vitamin *C* formation in *Hordeum* seedlings, its accumulation in etiolated seedlings upon illumination being more rapid than the process of chlorophyll formation. Giroud and others (160) have observed that the ascorbic acid (vitamin *C*) content parallels the concentration of chlorophyll in various parts of a green plant. Heller (193) claimed that a greater increase in vitamins *A* and *C* took place in germinating cereals exposed to the shorter wave lengths present in sunlight. According to Jansen (223), vitamin B_2, a flavine, is decomposed by light. An interesting relationship between vitamin and enzyme may be portrayed as follows: Vitamin B_2 + phosphoric acid + protein = yellow enzyme (cytochrome) of yeast (535).

In view of the known functions of ultra-violet radiation in the synthesis of vitamin *D* and in calcium fixation of animals, recent investigations of the chemo-synthetic activity of ultra-violet radiation in plants are of interest. Benedict (25) reported increased dry weight and increased per cent of calcium in tomato, corn, soy bean, cucumber and nasturtium grown with the ultra-violet region, 290–310 mμ, as compared with control plants receiving no wave lengths shorter than 310 mμ. Stewart and Arthur (524) also reported an increase in ash, and in calcium or phosphorus in plants exposed to brief daily periods of ultra-violet radiation. Cabbage, known to be lacking in antirachitic properties, did not respond to the treatment. The authors thought that the ultra-violet effective in fixation of the ash constituents exerted its influence indirectly by activation of the ergosterol present in the tissues of the plants. The chemical difficulties involved in experiments of this kind make

it difficult to interpret data on the basis of ultra-violet being the causal agent of the observed effects. It should be remembered that many kinds of plants have been grown to maturity in the complete absence of ultra-violet radiation without exhibiting any outstanding differences from plants receiving solar ultra-violet. Popp and Brown (402) have stated that out of 31 reports dealing with the effects of special ultra-violet transmitting glasses in greenhouses, unqualifiedly favorable results were given in only 8 cases and the data for these were not given or were of questionable value. Only slight differences have been found even in the most favorable reports, so that the use of special glasses for greenhouses is not to be recommended.

SEED GERMINATION

Seed germination in many species of plants is affected by light. About 1200 kinds of light-sensitive seeds have been reported and these include many of considerable economic importance (237, 357), such as species of *Poa,* lettuce, tobacco, etc. Some light-sensitive seeds continue their dormancy even after prolonged storage and refuse to grow unless exposed to light during the germination period; many others lose their need for light as a consequence of processes taking place in the seed during storage (300, 356); and still others, like the tomato, germinate better in darkness than in light (532). The question arises as to how photochemical processes may influence seed germination.

Honing (208) observed great variation in the need of light for germination in the different pure lines of *Nicotiana tabacum.* Results with reciprocal crosses between races of this species indicated that the need of light is a dominant characteristic, not of the seed coat, but of the embryo. Processes of after-ripening and the precise nature of the treatment during experimentation were found to be important in the determination of light sensitivity of *N. tabacum* and *N. rustica* varieties. The findings of Goodspeed (167), that some varieties germinated readily in darkness, may have been due to differences of genetic constitution or in the methods of experimentation so as to yield results at variance with those of Honing.

Schroppel (477) found that the respiration rate of germinating seeds of *Nicotiana tabacum* decreased in darkness. After a short

period of continuous illumination, their respiration rose rapidly and subsequently there followed a rise in the catalase and peroxidase activity. Since in light the acidity of fatty seeds of *Nicotiana* and *Verbascum* was found to be increased, Gardner (142) interpreted the phenomenon as due to splitting of fats to acids and glycerol by lipolytic enzymes activated in the light. Brief exposures to light (about 1 second at 200 meter candles) have been found effective in hastening germination of *Poa* sp. (300). However, germination of *Mimulus ringens* seeds exposed to weak light for long periods has been found to vary with the intensity, no germination taking place below 1.5 foot candles (217). The quality and quantity of the incident radiation which penetrates through the seed coat depend in part upon its absorption curve (18, 249). With equal energy values, the stimulatory effect of different wave lengths was found by Kommerell (249) to be proportional to the quanta of energy absorbed in the germinating seeds of *Lythrum salicaria* and *Nicotiana tabacum.* Recent studies of germination in lettuce have indicated that the blue region of the spectrum not only does not overcome dormancy but may actually induce it in normal seed (130). While short wave lengths inhibit germination, longer wave lengths in the orange-red region are effective in promoting germination. Shuck (493) claimed that non-dormancy may be retained in light-treated lettuce seed by drying the moist seeds in darkness.

Effects of ultra-violet radiation upon seed germination and early growth of seedlings have been investigated by many workers with diverse results and conclusions. Over a period of years, extensive experiments have been performed by Popp and Brown (*cf.* 402) using turnip, radish, cucumber, pigweed and curled dock. Different bands of ultra-violet were employed for irradiating the germinating seeds and the effects were recorded by the general appearance of the cultures, hypocotyl lengths, leaf measurements and dry weights. No significant stimulation was ever obtained when adequate controls were used. In a critical review of the literature on this subject, these authors (402) state that the only fact clearly demonstrated by experiments thus far carried out on the effect of ultra-violet radiation on seed germination and seedling growth is the injurious effect of short-wave radiation below 290 mμ. Evidence from more carefully controlled experiments indicates little

or no effect of the longer wave lengths of ultra-violet, *i.e.*, those from 290 to 400 mμ which are found in sunlight.

Applicability of the Bunsen-Roscoe rule for promotion of germination in Arlington Fancy lettuce seed has been tested by Flint (130). Over a relatively low intensity range of Mazda light the product rule seemed to hold true, but over the range 2 to 2048 f. c. at standard exposures of 1 second, the per cent germination increased from 0 to 86. In a more recent paper, Flint and McAlister

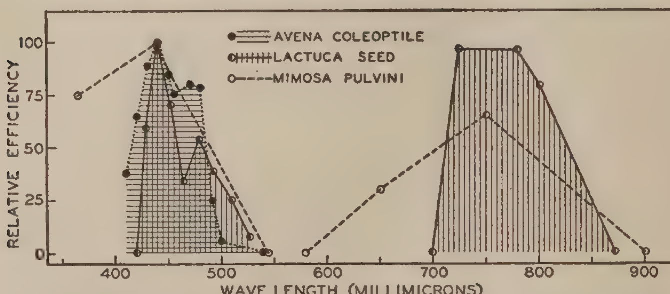

FIGURE C. The relative efficiency of different regions of the spectrum in bringing about phototropism, seed dormancy and photonasty in plants. Bending of the oat coleoptile toward light occurs chiefly in response to the shorter visible rays, as indicated by the dotted line and horizontal hatching. Germination of light-sensitive lettuce seed is inhibited by a band of radiation in the red and another in the blue region, as shown by the solid line and vertical hatching. The relative effectiveness of the short wave lengths of light in both of these phenomena is represented by bimodal curves with maxima in the regions 440 and 480 mμ. The induction of seed dormancy by red light is not paralleled by phototropic response to the same rays. However, the activation of *Mimosa* pulvini by blue-violet and also by red wave lengths shows some similarity to the effect of light upon lettuce seed. Further study might show a relationship between the processes involved in phototropism, photonasty and seed dormancy. Data for the *Avena* coleoptile have been taken from Johnston (228), for *Lactuca* seed from Flint and McAlister (131), and for *Mimosa* pulvini from Burkholder and Pratt (62)).

(131) have demonstrated that a band of radiation in the region of 760 mμ and another in the region 420 to 520 mμ inhibits germination of this same variety of lettuce seed. On the other hand, the yellow-orange wave lengths promote germination. The relative effectiveness of narrow bands of shorter wave lengths of visible light was found to be similar to the spectral sensitivity curve for phototropism in etiolated coleoptiles of *Avena* (228). It is significant that the spectrum curves for induced dormancy in lettuce

seed and phototropism in *Avena* should show maxima at about the wave lengths of 440 and 480 mμ which are known to closely approximate the absorption maxima of carotenes (*cf.* 322).

The long red wave lengths which inhibit germination are effective in provoking response in *Mimosa* (64). The action of light in phototropic phenomena is known to be concerned with the function of certain specific substances, auxins (*cf.* 247), and, moreover, nastic movements of *Mimosa* can be influenced also by application of hetero-auxin (247) to the pulvini (64). Whether auxins have any rôle in connection with the phenomena of dormancy and germination of seeds remains to be proven.

The necessity of water and available oxygen during exposure to light for the accomplishment of the light effect has been emphasized (39, 477, 586). Working with selected kinds of plants, Böhmer (39) found that germination of light-inhibited seeds was favored by a higher partial pressure of oxygen than that of the normal atmosphere, but that germination of light-favored seeds was inhibited by higher oxygen, while light-indifferent seeds remained unaffected by considerable variations in the oxygen partial pressure.

Light sensitive *Lythrum salicaria* seeds, which had been kept in an atmosphere of nitrogen or of hydrogen, showed much better germination subsequently than did seeds which had been kept in an atmosphere containing oxygen (541). Several investigators (*cf.* 39, 493) have obtained evidence suggesting the existence of a photosensitive substance in light sensitive seeds, but as yet no specific chemical substance has been identified in this connection.

GROWTH-SUBSTANCES

Experiments dealing with growth behavior of plants in relation to light have, in some instances, yielded results not to be explained on the basis of variation in supplies of fundamental constituents, such as minerals, water and carbohydrates. Searches for satisfactory explanations of certain puzzling phenomena have led to the discovery of many special substances including enzymes, vitamins, hormones, etc., which play specific rôles in physiological processes. Some effects of light which appear to be exerted through formation and activity of special growth-substances have been worked out in a rational manner in the last several years. Many early investigations, including those of Darwin, Sachs, Boy-

sen-Jensen, Paal, Söding, and others (*cf.* 52), gradually built up a fund of information which strongly suggested the existence of specific growth-promoting substances, but only in recent years has definite progress been made in the direction of their qualitative and quantitative determination. Went's (577) paper on the quantitative determination of growth-substance gave a new impetus to investigations which have yielded remarkable discoveries. At Utrecht, Kögl and his associates (247) have discovered and prepared in pure form several substances which promote plant growth, it is believed, mainly through increase in cell size. These substances have been called *auxins*. The relation of light to the rôle of growth-substance action in plants is as yet poorly understood. Went (577) found a decrease of 18 per cent in the amount of growth-substance given off by the coleoptile of *Avena* when illuminated with 1000 m.k.s. as compared with plants kept in darkness. Küstner (261) observed that the activity of growth-substance prepared from urine was increased by red light, and decreased by shorter wave lengths. Navez (347) was able to demonstrate an increased amount of growth-hormone in apical portions of *Lupinus albus* seedlings subjected to weak Mazda light. Etiolated *Raphanus* seedlings lose the ability to form growth-substance, while plants kept in the greenhouse retain their synthetic power for for a long time, according to Van Overbeek (374). Avery (17) found that a growth-hormone was produced in young growing leaves of tobacco in the light, but in darkness it disappeared after several days. The data of Chesley (75), who reported that wheat seedlings sprouted in the light were less sensitive to X-radiation (which destroys auxin (500)) than those germinated in darkness, may be interpreted on the supposition that a greater concentration of auxin was present in the illuminated plants, and hence greater doses of X-rays were required to check their growth. Went (581) has stated that "only in seedlings is growth-substance formed in the dark, apparently from reserves in the seed." That light may indirectly have some relation to the manufacture of substances which promote root formation may be inferred from experiments of Went (578) with *Acalypha* cuttings, where roots were formed in greater numbers when expanded leaves or buds were present on the shoots. In a later paper, Went (580) states that "in plants with leaves in the light, root formation goes on during weeks and

no constant level of root formation is reached, indicating that in leaves we have to do with new formation of rhizocaline," a root-forming substance. Red and orange wave lengths appear to be especially effective in the production of rhizocaline, though light seems to inhibit its action (582). Laibach (262), Müller (339) and others have shown that roots are formed abundantly on cuttings to which growth-substance has been applied. Presumably, light is essential for synthesis of growth-substance in plants, and the nature of photochemical reactions involved await thorough investigation.

ELECTRICAL POTENTIAL

The fundamental nature of the polar axis in plants has been one of the great morphogenetic problems since the time of Sachs (453) who postulated the presence of shoot- and root-forming substances to account for axial differentiation. Vöchting (560, 561) and others have demonstrated that not only gross structures but also individual cells of the plant body possess definite polarity. Experimental results of many investigators in recent years have given good reasons for believing that morphological polarity is related to electrical polarity.

Since electrical potentials in plants were described at length by Bose in 1907 (46), a vast amount of experimental data has accumulated on the subject (*cf.* 29, 274, 372, 522, 445). The power of light in the production of electric currents was very well demonstrated in one of the experiments described by Bose (47). Two halves of a banana leaf, severed along the midrib, were immersed in a dilute salt solution and wire leads were connected to form an external circuit through an electrometer. When one leaf portion was illuminated and the other kept in darkness, the system behaved as a photoelectrical cell and a flow of current was registered on the sensitive indicator. Waller (565) experimented with photoelectric effects in green, albino and etiolated tissues, and came to the conclusion that chlorophyll was the active agent in the responses observed. In a later paper by the same author (566), the bioelectric current was attributed to lack of equilibrium between oxidative and reductive processes. Most leaves showed an initial negative phase upon illumination but etiolated leaves and others kept in darkness for a number of hours gave an initial positive phase.

Sheard (489) has reported induced potentials which attained a maximum of the order of .1 volt in the leaves of sunflower and poinsettia exposed suddenly to ultra-violet or infra-red radiation. Glass (162) used excised green leaves of *Elodea* and measured the potential produced by an intense spot of light applied locally to different regions along the midrib. When the apex of the leaf was illuminated, a potential difference of about 100 millivolts was found between the apex and base, the former being positive in the external circuit. When the spot of light was applied to the base only, this region became positive (external circuit) to the darkened apex. Transmission of the effects of light to non-illuminated regions in the plant was obvious from the experimental results. The author was of the opinion that the effect of light upon E. M. F. in the leaf was not a direct photoelectric effect but, through action of light on the chloroplasts, changes of state were set up which gave rise to the electric phenomena. Experiments of Brauner (54) with *Hordeum* have shown that unilateral light sets up a negative potential on the lighted side. This discovery has considerable significance in the theory of tropisms which are now explainable on an electrical basis. Some of the ways in which electrical polarity may give rise to profound morphological effects in the plant will be referred to under the discussion of morphological differentiation.

That light may have direct action upon physical properties of the minute structure of the cell has been suggested by several investigators. Hercik (195, 196) interpreted the rise in surface tension of cell sap in etiolated seedlings after illumination as a photoelectric phenomenon similar to the Hallwach's photoelectric effect (*cf.* 592) where negatively charged bodies lose their charges upon illumination. When the negative particles of sap lost their charge in light and surface tension was raised, Hercik called it a positive photocapillary reaction.

Overbeek (374) has put forth a theory to explain direct inhibition of light upon cell-wall-stretching on the basis of photoelectrically altered charges on the intermicellar substance which is believed to be charged oppositely to that of the cellulose layers of the wall so as to hold the pattern in a more or less rigid position. According to Overbeek's theory, the light quanta which are absorbed by cell walls would tend to increase the potential difference between the cellulose and intermicellar substance, and thus render the wall

less stretchable and less susceptible to the action of growth-substance. It may be of interest in passing to mention that Chouchak (77) found that in the light, leaves bearing a positive charge absorbed more CO_2 than those having a negative charge, thus influencing the process of photosynthesis.

To account for polar distribution of growth-substance, Went (579) proposed the theory of electrical potential in plants, according to which the charged particles or ions are attracted in the direction of unlike charge. Recently, distribution of the growth-hormone in plants has been demonstrated experimentally on the basis of electrical potential. Ramshorn (419) and Koch (246) found that negatively charged ions of growth-substance migrated toward the positively charged region in the organs of the plant (as it did also in agar) and there exercised its rôle in causing tropistic growth responses. Since light is known to be active in the formation of potential gradients in plant tissues, it is obvious that the light factor must have a significant effect upon growth by exercising an indirect influence upon distribution of specific growth-substances.

In view of modern developments in this field of research, it is apparent that light has profound influence upon polarized and general growth, and upon processes concerned in differentiation of the plant body; but the mechanism is by no means completely understood. Growth and developmental characteristics which appear as responses to variations in the light environment suggest specialized types of internal chemical reactions and physical conditions, but it is difficult to discover the latter and show the complete history of the case from environmental stimulus to morphological response.

A profound morphogenetic influence of light upon the polar growth gradient in higher plants has been suggested by recent work concerning growth and inhibition of lateral buds by auxin (536). Also Kahane (230) has shown that either in the presence or in the absence of CO_2, light could condition normal development of axillary buds of true leaves and repress the cotyledonary buds in pea seedlings, while in darkness, vigorous growth occurred from the axils of the cotyledons. Garner and Allard (146) pointed out that in a day length below optimum, apical dominance may be diminished so that the leaf rosette or branching habit develops in place of the erect form. In *Cosmos* and *Poinsettia,* grown under

long days, there was a tendency for foods to go toward the upper part of the plants. Under favorable light conditions, carbohydrates stored earlier in tubers and thickened roots were translocated upward for growth in stature of the shoot. Experiments with *Ullucus tuberosus* and *Oxalis tuberosa* (425) have indicated the possibility for certain effects of localized photoperiodic stimulation to be readily transmitted morphologically downward but not upward. Investigations of Garner and Allard (146, 147) have given indication of transmitted photoperiodic influence only under certain specific conditions. Proof of the formative effects exercised through electrical potential has recently been given by important experiments of Schechter (467), working with the red alga *Griffithsia.* This investigator was able to bring about regeneration of rhizoids on the induced positive end, and vegetative shoots on the induced negative end of isolated portions of the alga grown in sea water in an electro-culture chamber. From the experimental results, it may be inferred that formative substances may be differentially distributed under conditions accompanying normal polarity in plants, and in this manner differential growth patterns may be initiated and maintained. Recent discoveries concerning the hormonal nature of the cambial stimulus (510, 511) and the downward movement of cambial activation in woody plants (412, 537) suggest that light, through its influence upon growth-substance formation, and electric polarity, through its action in causing differential distribution of these ionized substances, may be of much greater importance for morphogenesis than hitherto realized.

Bibliography will appear with the second part of Dr. Burkholder's article in the March issue.